

BREEDING BIOLOGY OF AMERICAN COOTS IN IOWA*

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ALTHOUGH the American Coot (*Fulica americana*) has been intensively studied by several investigators, many facets of the breeding biology of the species have not been explored. This paper presents observations on the species in Iowa, made during an experimental study of clutch size in the coot (Fredrickson, 1969).

Sooter (1941) conducted intensive studies on coots in northwestern Iowa. Gullion, who studied a small resident population of coots in California, has made the most detailed observations on the breeding cycle. His publications describe voice differences between the sexes (Gullion, 1950), histology and development of the frontal shield (Gullion, 1951), sex and age determination (Gullion, 1952a), molt (Gullion, 1953a), territorial and courtship activities (Gullion, 1952b), and seasonal variation in interspecific and intraspecific territorial activity (Gullion, 1953b). Gullion (1954) summarized his observation on the reproductive cycle of coots in California and compared his findings with information available on other Rallidae. Nest-building, laying, incubation, and hatching were described in detail, but pairing, copulation, and brood-rearing were discussed less thoroughly.

STUDY AREA

The study area was in northwestern Iowa near Ruthven, a marsh area studied and described in detail by Bennett (1938), Low (1945), and Glover (1956). Coots were studied on three marshes, all of glacial origin but modified so that water levels were controllable. The dominant vegetation was cattail (*Typha* sp.), which provided the major nesting cover for coots and other species that nest over water.

METHODS

Nests were located each year by systematically wading or canoeing the marshes. Initiation dates of nests found during laying were calculated by allowing one egg per day. The initiation date was not calculated in nests located during incubation, but embryonic development was appraised by floatation (Westerskov, 1950) or candling (Weller, 1956) as an index to the stage of incubation.

Adult coots were captured for banding and color-marking by using three techniques: nest-trapping, night-lighting, and bait-trapping.

Automatic nest-traps similar to those designed by Weller (1957) generally were successful late in the incubation period; occasionally, however, some birds were captured shortly after laying stopped. Some coots were less broody than others and avoided entering a trap at any time. Thus, the individual broodiness of a coot determined the success of nest-trapping.

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Night-lighting was effective for capturing nesting birds when the study area and nest locations were well known. The technique worked best on dark nights. Coots were most easily caught with a small-sized dip net made of fine "mist" netting. The birds became entangled in the mist netting which allowed fewer to escape. The maneuverability of the light-weight net in the floating vegetation increased the efficiency of capturing coots. If the exact location of the nest and ramp was known before the night-lighting attempt, the incubating coot could be captured as it left the nest.

Gullion's (1950) method of differentiating sex by vocalizations was used. The higher-pitched call of the male is easily distinguished from the lower-pitched notes of the female. With experience, coots also may be sexed by comparing body size, and shape and size of the frontal shield and bill (Gullion, 1951; Fredrickson, 1968).

Adult coots were banded with Fish and Wildlife Service bands and were color-marked in two ways. Each bird was marked with three colored plastic leg bands and a patagial tag, or a nasal saddle, which was visible when the bird was swimming.

The patagial tag was similar to one described by Anderson (1963) but was attached to the patagium by a slightly different method. Either a stainless steel welding rod ($\frac{1}{16}$ -inch diameter) or a stainless steel wire was passed through the patagium and the ends flattened or looped beyond plastic washers to hold the tag in position. The tag was made of a double layer of plastic with colors providing individual identification.

In 1966 nasal saddles (Sugden and Poston, 1968) were used rather than patagial tags. A saddle-shaped piece of plastic was placed over the culmen in the region of the nares. A $\frac{1}{16}$ -inch diameter stainless steel welding rod was passed through the holes bored in the plastic and through the nares of the bird. The ends of the rod were flattened to hold the saddle in place. Color patterns on the tabs identified individuals.

TERRITORIAL BEHAVIOR

Gullion (1952*b*) described territorial behavior and reviewed the literature on aggressiveness in coots. My observations support Gullion's findings. I prefer the term "Chase" over *splattering* but use the terms "Patrol," "Charge" and "Paired Display" as described by Gullion.

I attempted to determine the intensity of the territorial displays and to determine if displays were used in a particular sequence. Intensity was determined by the frequency of display, with displays of lowest intensity occurring most often.

Figure 1 shows the pattern of displays in 30 complete sequences observed in my study. As many as eight displays have been recorded in a sequence. In 27 of the 30 observations, four or fewer displays were involved in each sequence. In 24 sequences, the low intensity Patrol was the initial display. In nine of the 24, the intruder retreated and the contest ended. On some occasions the initial display was of greater intensity than the Patrol. For example, both Charging and Chasing were observed as the initial display. Of 19 sequences with more than one display, eight ended in Paired Display, seven ended in Chase, three ended in Patrol and one ended in Charge.

Coots usually concluded each display sequence with a quick dive regardless of length or intensity of a sequence. On a few occasions the feathers were

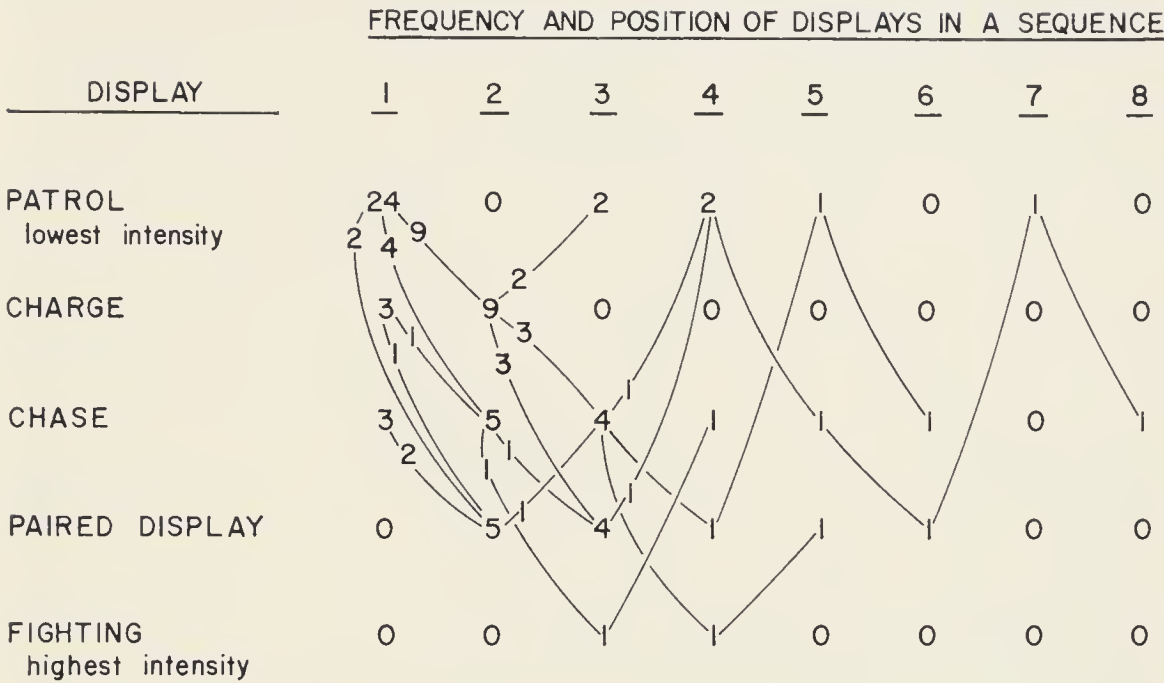


FIG. 1. Frequency of displays observed in territorial activity of the American Coot.

straightened by a Shuffle following the dive. This activity did not occur regularly in the sequence, but occurred commonly during feeding or swimming. Evidently it arranged the feathers over the entire body. The bird moves upward and forward above the water surface. Simultaneously, the wings are elevated slightly above the body. As the head falls forward, the rear portion of the body rises above the water as if the bird were moving over an obstruction. The breast region makes contact with the water first, and the movement ends when the wings return to the normal position.

Several observations of interspecific aggression were made during this study. The degree to which this aggression occurred seemed correlated with the stage of the nesting cycle. Both Mallards (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*) were driven from the coots' territory in May. Neither Ruddy Ducks (*Oxyura jamaicensis*) nor Redheads (*Aythya americana*) were attacked when encountered late in the nesting season.

REPRODUCTIVE BIOLOGY

Nest and platform construction.—Platform construction is a well-known behavior of nesting coots. Gullion (1954) reported that three pairs constructed as many as nine structures associated with nesting during a single season. Other reports on nest construction were by Wetmore (1920) and Walker (1932) and by Kornowski (1957:341–342) for the European Coot (*F. atra*). In my study, platform building was influenced by the availability of naturally-occurring platforms in the marsh. Coots used muskrat lodges,

TABLE 1

USE OF COVER-TYPE VEGETATION AS NEST MATERIAL BY COOTS IN THE RUTHVEN AREA
IN 1963 THROUGH 1966

Cover-type vegetation	Nest material						Total
	Same as cover-type	Cattail	Cattail and softstem	Cattail and other species	Softstem	All other species	
Cattail	255	255	44	10	8	3	320
Softstem	16	—	—	1	16	—	17
Cattail and softstem	18	—	18	1	8	1	28
Softstem, river bulrush and cattail	—	—	—	—	1	—	1
Cattail and river bulrush	—	—	—	3	1	—	4
River bulrush	3	—	—	—	1	3	3
Hardstem	—	—	—	1	—	—	1
Cattail and sedge	1	1	—	—	—	—	2
Willow	—	1	—	—	—	—	1
Burreed	—	1	—	—	—	—	1
Cattail and hardstem	1	—	—	—	—	—	1
Total	294	258	62	16	35	8	380

feeders, and latrines extensively and built fewer platforms when structures built by muskrats were plentiful.

In my study, nest-building was conducted by both sexes of a marked pair. One bird carried material to the nest site while the mate constructed the nest. The construction and collection activities were often interchanged between the sexes. Although coots used structures built by other species for loafing, copulation, and brooding, all 565 nests in my study were built exclusively by coots.

Coots are very adaptable and will use a variety of materials in nest construction. Possibly dry materials are favored over wet materials, because one pair of marked coots bypassed masses of readily-available floating cattail stalks and traveled to a muskrat lodge to secure dry cattail stalks.

Coots did not appear to favor a particular vegetative type for nest materials. The available material was used regardless of species and whether it was cured or green. Cured material was used most commonly. Cover type and nest material were recorded for 380 nests (Table 1). Of this number, 294 were constructed exclusively of material that existed as cover around the nest.

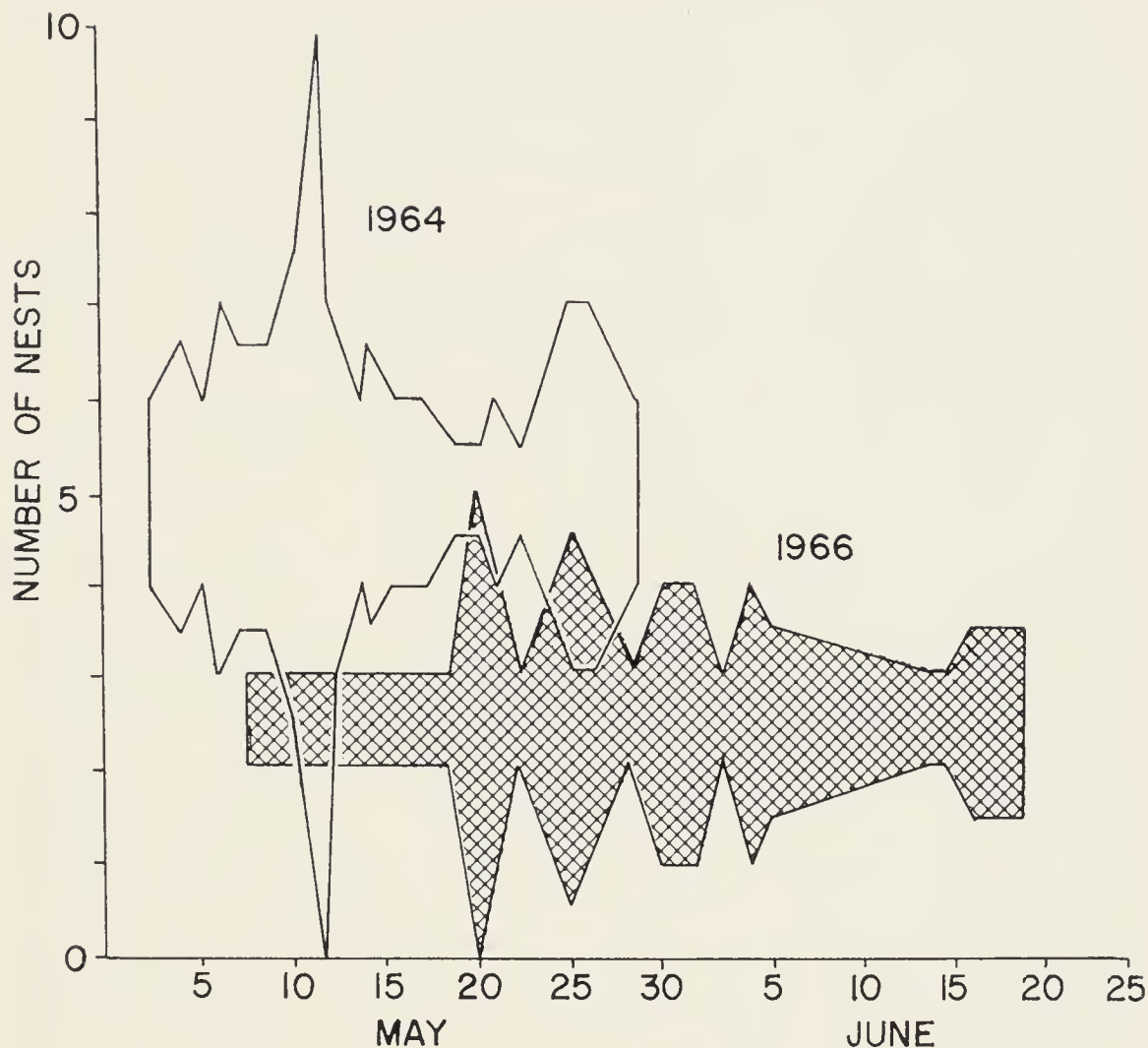


FIG. 2. Chronology of initiation of laying by the American Coot during 1964 and 1966.

Three hundred twenty nests were built in cattail, the most common cover type in these marshes. Of these 320 nests, 255 were built entirely of cattail. Eleven of the nests in cattail were constructed entirely of some other plant species: eight of softstem bulrush (*Scirpus validus*), two of softstem bulrush and arrowhead (*Sagittaria* sp.), and one of river bulrush (*Scirpus fluviatilis*).

Chronology of nesting.—The chronology for initiation of laying was determined in 1964 and 1966 but not in 1965. Dates of initiation were determined either by direct observation or by calculation of the initiation date as described earlier. In 1964, the first nests were recorded on 3 May, with the first peak of initiation of laying occurring on 11 May (Fig. 2). A second peak of initiation occurred 2 weeks later on 25 May. Although coots in California may have two nests each season, no evidence was found that indicated this possibility in Iowa. This second peak may represent reneesting or possibly late nests of young birds.

Nest chronology in 1966 differed from that found in 1964. Unusually cold weather in May probably kept the birds in a nonbreeding condition. The first laying occurred 1 week later than was expected. No well-defined peak of initiation of laying occurred during the season, and nest initiation lasted until mid-June (Fig. 2).

Some coots did not nest until new vegetation was sufficiently high to provide nest materials and a substrate for attaching nests. On two marsh areas near Ruthven, small flocks of coots had territories located in areas with little or no nesting cover until after late May. Coots in one flock began to nest when a dense bed of sweet flag (*Acorus calamus*) had grown to a height suitable for nest attachment. Peak of nesting occurred on this area about 25 June, or 6 weeks later than the first peak (11 May).

Another flock of coots centered their activity in a sparse stand of cattail that was in poor condition due to a muskrat eat-out and flooding. Twenty-five nests were eventually initiated in the area. But the first egg was laid on 18 May, or 15 days after the first eggs were laid in optimal habitat with taller and more dense vegetation. As the cattail developed, more nests were established, and the peak of initiation of laying occurred on 29 May. No nests were initiated later than 21 June. Twenty-three nests with completed clutches of eggs had an average clutch size of 6.3 (range, 3–10 eggs). Of the 25 nests, 9, or 36 per cent, hatched successfully, 7 were destroyed by unknown causes, and 8 were deserted. The fate of 1 nest was not determined.

Copulation.—Observations on copulatory behavior were recorded to determine the seasonal occurrence and the sequence of displays normally involved in this activity. My observations agree with Gullion's (1954:373). Copulatory activity extended over about 1 month, but probably occupied a shorter period of the cycle of each pair. All records of copulation occurred between 13 May and 2 June. Some nests were initiated in early May so copulation must have occurred earlier for some. The period of copulation was closely associated with the egg-laying period. Once a female completed her clutch, copulation was rarely seen. Copulatory attempts, by males, were observed as late as 19 June. Similar findings were reported by Lelek (1958) for the European Coot.

Laying.—The normal pattern of laying has been described by Sooter (1941) and Gullion (1954) who agreed that American Coots lay eggs at intervals of slightly more than 24 hours. Gullion reported a 48-hour gap between two eggs on two occasions, but two eggs were laid on the day following one of these long periods. Sooter (1941) reported that two eggs were laid in two nests in 1 day. These data would be influenced by the recording time and may not reflect the true interval between laying.

Because coots are usually very aggressive, it seemed unlikely that females could avoid the intense territorial defense of most coots to lay eggs in a nest

TABLE 2
DATA ON CLUTCH SIZE OF THE AMERICAN COOT

Clutches				
Number	Range	Mean size	Location	Source and date
169	5-13	9.9	Manitoba	Kiel (1955)
104	1-11	6.08	Iowa	Sooter (1941) for 1936
347	4-18	7.92	Iowa	Sooter (1941) for 1937
15	6-16	8.93	Iowa	Present study 1963
87	6-17	9.85	Iowa	Present study 1964
81	6-13	9.23	Iowa	Present study 1965
98	4-13	8.16	Iowa	Present study 1966
281	4-17	9.03	Iowa	Present study overall mean
8 ^a	7-10	9.0	California	Gullion (1954)
5 ^b	4-8	6.4	California	Gullion (1954)

^a Early season clutches.
^b Late season clutches.

in another territory. It is known, however, that birds of other species do occasionally lay eggs in coot nests. Ruddy Ducks occasionally lay eggs in coot nests (Weller, 1959 and present study). In South America the Black-headed Duck (*Heteronetta atricapilla*) lays eggs in the nests of several species of coots and other birds (Phillips, 1925; Weller, 1968). Promiscuous laying occurs in the European Coot (Alley and Boyd, 1947) and this suggests that similar behavior might occur in the Nearctic form.

Evidence from this study suggests that more than one female might lay eggs in the same nest. Two eggs were added to a nest on 3 consecutive days. The pair associated with nest was marked, and no other coots were observed on or near the nest. Observations on the nest were not continuous, but it seems unlikely that all eggs were deposited by a single female.

Another nest contained 12 eggs; 4 of these eggs were slightly different in shape, were darker in color, and had a different pattern of black flecks than the other 8 eggs. A recent paper by Labisky and Jackson (1966) indicated that caution must be used when associating egg color with a particular female because eggs of the Ring-necked Pheasant (*Phasianus colchicus*) were variable for each hen studied. Because the development of the four eggs lagged a week behind other eggs in the clutch, parasitic laying probably occurred.

In this study, I assumed clutches were the product of two or more females when clutches were in excess of 12 eggs, when eggs were of different sizes or shapes and when two eggs were laid on the same day.

Clutch size.—I examined 565 coot nests. For 281 nests the mean clutch

TABLE 3
FREQUENCY OF OCCURRENCE OF CLUTCH SIZE IN THE AMERICAN COOT IN NORTHWESTERN
IOWA IN 1963 THROUGH 1966

Clutch size	Number of nests					%
	1963	1964	1965	1966	Total	
4	0	0	0	3	3	1
5	0	0	0	2	2	1
6	1	3	3	9	16	6
7	4	7	5	22	38	14
8	1	7	15	24	47	17
9	5	17	22	17	61	22
10	2	25	27	14	68	24
11	1	17	3	2	23	11
12	0	6	4	2	12	4
13	0	2	2	3	7	2
14	0	1	0	0	1	—
15	0	1	0	0	1	—
16	1	0	0	0	1	—
17	0	1	0	0	1	—
Total	15	87	81	98	281	—

varied as follows (Table 2): 1963—8.93 (s.d. ± 5.99), 1964—9.85 (s.d. ± 2.16), 1965—9.23 (s.d. ± 1.67), 1966—8.16 (s.d. ± 1.87), and overall mean 9.03 (s.d. ± 2.01). A null hypothesis of no differences between the means was tested with Duncan's new multiple range test (Steel and Torrie, 1960). At the 5 per cent level, the clutch size of 9.85 in 1964 was significantly larger than the clutch size of 8.16 in 1966.

The frequency distribution of clutch size in nests studied from 1963 through 1966 is summarized in Table 3. These data show that clutches with more than 12 eggs or less than 7 eggs were uncommon. Clutches of 10 eggs occurred most commonly, but clutches with 9 eggs were nearly as common. The data presently available on clutch size in the American Coot are inadequate to determine if variations exist in clutch size because of geographical location (Table 2).

Clutch size of the American Coot does vary seasonally. Late clutches in California average 6.4 eggs (Gullion, 1954), or 2.6 fewer eggs per clutch than in early clutches. Much of Sooter's data probably reflect the smaller clutches in late nests. Data collected on clutch size during the 4 years of my study were plotted against time (Fig. 3). Early clutches tended to be larger than late clutches. When the average clutch size was calculated on a weekly basis starting with the first of May, an average of 11.1 eggs per clutch for the

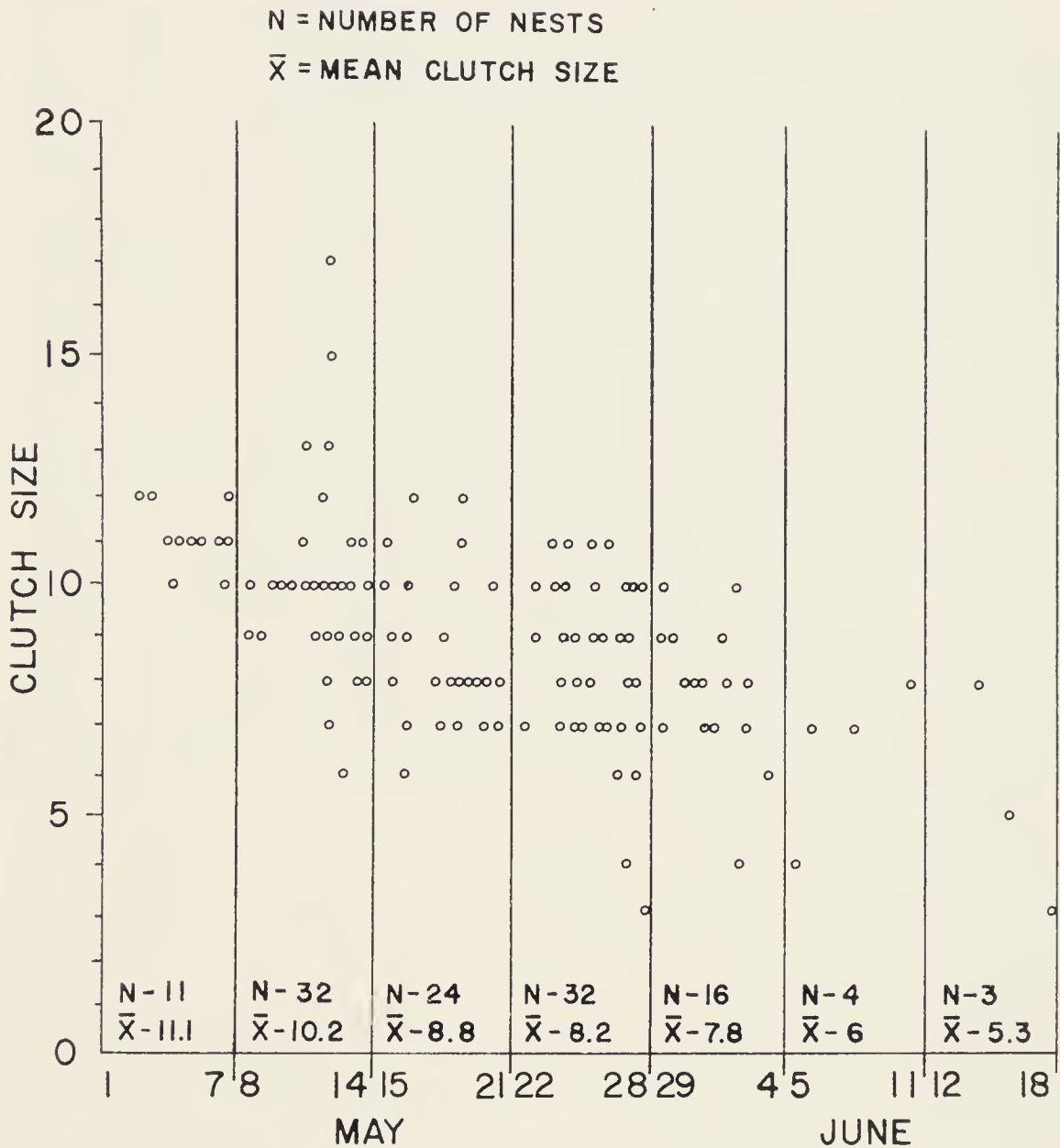


FIG. 3. Clutch size in relation to date of initiation of laying.

first week of May dropped to an average of 5.3 eggs per clutch for the seventh week of nesting. A null hypothesis of no differences between the means for the 7 weeks was tested with Duncan's new multiple range test (Steel and Torrie, 1960). At the 5 per cent level, the following comparisons were significantly different: 11.1 from all means of 8.8 or less, 10.1 from all means of 7.8 or less, 8.8 from all means of 6.5 or less, and 7.8 from all means of 5.3 or less. Similar data have been reported for Blue-winged Teal (Bennett, 1938) and for other dabbling ducks by Sowls (1955). The smaller clutches appearing later in the season may be the result of renesting or of first nests of young birds.

Incubation behavior.—Researchers studying the American Coot have not agreed on the time of initiation of incubation in relation to the number of eggs in the nest. Sooter (1941) reported that incubation commenced with the first egg, but he did not present supporting evidence. Gullion (1954) observed that incubation began with the first egg only on second clutches. In first clutches, initiation of incubation was variable: some birds started incubation after two eggs were laid, but others completed the clutch before incubating (Gullion, 1954:377). My observations indicated coots spent some time on the nest as soon as the first egg was laid, but evidently incubation was insufficient during the first 3 or 4 days of laying to induce embryonic development. Eggs were generally cold in nests with less than four eggs, but eggs were usually warm in nests with four or more eggs. A similar situation has been recorded for Red-fronted and Red-gartered Coots (*Fulica rufifrons* and *F. armillata*) in Argentina (Weller, 1968:194). Eggs usually hatched over a period of several days, but the appearance of three or four young during the first day of hatching is the result of this incubation behavior.

Because laying and incubation occurred during the same period, some confusion has resulted in determining the length of incubation. Gullion (1954:383) studied this problem closely on four nests by marking eggs as they were laid. The eggs hatched in 23 days. My data are not directly comparable with Gullion's because I used the Heinroth method (interval between the last egg laid and the last egg hatched) to determine the incubation period. Only three nests were checked frequently enough to determine incubation of 23, 24 and 27 days. Four other nests were known to have hatched between 21 and 25 days.

Both members of the pair share in incubation. According to Gullion (1954:378), the male was most often on the nest during the night and for a few short intervals during the day. In 11 observations during my study a nest-changeover ceremony was never recorded, but the possibility of vocal signals cannot be ruled out even though no evidence is presently available to support this possibility.

In eight of the changes observed, one member of the pair had left the nest before the arrival of the mate. In all eight observations the identification of sex was positive. When the incubating bird entered the nest, it preened its breast and belly regions from one to 9 minutes before settling on the eggs.

Brooding.—Because all eggs in the clutch do not hatch simultaneously, coots must continue to incubate but also must feed and brood the young that have hatched. Newly-hatched coots are capable of movement (precocious) and are covered with down (ptilopaedic) and are able to leave the nest as soon as they are dry (nidifugous). Nice (1962) places the rails in her Precocial Category IV, which includes chicks that follow their parents and

are fed by them. Both parents shared in brooding the young, but one of my observations on two marked pairs indicated that the male had a greater share of the brooding responsibility. After all the eggs had hatched young coots traveled with both parents during the day and did not appear to favor one sex. At dusk, when broods moved to platforms, the male seemed to assume the responsibility of caring for most of the young. Observations on two broods with marked adults indicated that in both cases the males brooded five and 10 young respectively and the females remained nearby without young.

Young birds were particularly prone to wetting for a few days following hatching. Feathers of the young birds were oiled directly by billing movements of the adults from their preen glands to the young. Adults also oiled their young by rubbing their oiled underwing and breast feathers on the newly-hatched young. Wild young with parents appeared less prone to wetting than were captive birds that were reared without parental care.

As soon as young coots were dry, they pecked at egg shells and larval insects dropped in the nest. When adults approached, the young birds begged vigorously. The wings were outstretched and moved rapidly in a vertical plane. The head was raised and rotated backward so that the occiput rested against the back or was held directly above it. The head usually moved from side to side.

During the first days following hatching, the young coots appeared dependent on the parents for food. Both sexes collected food for the brood. When one member of the pair was feeding the young at the nest, the mate collected food and then presented it to the incubating bird which in turn fed the young. Larvae of aquatic insects and small crayfish were foods commonly fed to chicks.

Nest sanitation.—Both sexes removed egg shells and vitelline membranes from the nests soon after the young hatched. The adults either ate the egg shells or carried them from the nest and dropped them into the water. Egg shells eaten at the nest accounted for many of the small chips usually associated with successful coot nests.

SUMMARY

Both sexes of the American Coot share in nest construction. Coots used a variety of nest materials but seemed to use materials readily available, particularly dry materials.

The number of platforms constructed by coots during a breeding cycle may depend on the availability of other structures in the marshes such as lodges built by muskrats. Even though coots used other structures for brooding and copulation, coots always constructed their own nests.

Cold spring weather appeared to delay breeding and reduce the average clutch size from 10 to 8. Coots also were influenced by habitat conditions. Birds nesting late in

suboptimal habitat tended to have smaller clutches. It was not known whether this was because of the habitat or merely reflected the physiological condition of birds associated with a particular habitat. In either case, these clutches not only contained fewer eggs but had a lower nest success than birds nesting in good habitat.

Soon after hatching, the parents either ate the egg shells or carried them from the nest and dropped them in water. Because eggs in coot nests hatched over a period of several days, both brooding and incubation behavior were conducted simultaneously. During the first week after hatching, young birds were fed large quantities of aquatic insects and were brooded by the parents. Males appeared to do most of the brooding at night.

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